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Pox and Plumage Coloration in the House Finch: A Critique of Zahn and Rothstein

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Documenting effects and then establishing their causes lie at the heart of scientific investigation. In a recent study, Zahn and Rothstein (1999) presented evidence that the mean plumage redness of male House Finches (*Carpodacus mexicanus*) in coastal California has decreased over the last 100 years. They then argued that the sole cause of that change in plumage redness was an increased incidence of infection with avian pox. Finally, they looked at current geographic variation in mean male plumage redness and argued that the observed patterns were the result of differential exposure to a pox virus. Unfortunately, the authors did a poor job of documenting the effects that are the focus of their study, and then they proposed an overly simplistic cause for the purported effects.

The House Finch has become a model species for studies of the function and evolution of ornamental plumage coloration (e.g. Olson and Owens 1998, Hill 1999). Male House Finches have carotenoid-based ornamental coloration on the crown, breast, and rump that varies in coloration from dull yellow to bright red. If degree of infection with pox explained most of the variation in expression of male plumage coloration in House Finches as proposed by Zahn and Rothstein (1999), that finding would have important implications for our understanding of carotenoid-based ornamental plumage coloration in the House Finch, in particular, and in birds in general. I believe, however, that the methods employed by Zahn and Rothstein (1999) were sufficiently flawed that the conclusions from their study are questionable.

Careful quantification of plumage hue was central to Zahn and Rothstein's (1999) study, but their method of scoring plumage coloration was somewhat baffling. The coloration of male crown, breast, and rump was first scored by comparison with color chips in Smithe (1975), which is essentially a haphazard collection of color chips (i.e. it is not organized along tri-stimulus color axes). The numbers obtained from Smithe (1975) were then matched to chips in the Munsell color system (Munsell 1976), which is far superior to Smithe (1975) as a standard color reference because it has many more intermediate colors that are arranged along tri-stimulus axes. However, the greater number of color chips and superior arrangement of chips for assessing color variation are pointless when all color observations are first filtered through Smithe (1975). As a last step, color scores were divided into three broad categories: yellow, orange, and red. That method of color quantification is analogous to recording the wing length of a bird using finger widths, measuring the finger widths with a ruler, then calling the bird large, medium, or small. No one would accept that as a suitable way to measure size in a study. Why should an equally bad approach be accepted for measuring color, particularly when much better methods are available (Burley and Coopersmith 1987, Zuk and Decruyenaere 1994, Hill 1998)?

Even if we accept the coarse color-scoring methods of the authors as a suitable means of detecting differences in plumage coloration among populations, the authors' approach to documenting temporal and geographic variation in mean male coloration and then linking the purported change to pox was unconvincing. First, consider whether the mean plumage redness of male House Finches has decreased over time in coastal California. The authors test for an increase in pox over time by dividing birds into those collected before 1960 and those collected after 1960 and looking at the proportion of red males in each group. The rationale for that cutoff is the discovery of the pox virus infecting House Finches in California in 1972. Thus, instead of establishing an effect (change in plumage coloration over time) and then searching for a cause, the authors used their preconceived notions about the purported cause (pox) in how they defined the effect. That approach makes for poor science. Moreover, the 1960 cutoff that was used for including birds in the pox group is not justifiable, even if the lack of specimens from the 1950s makes that a convenient cutoff. As the authors acknowledged, pox was not detected in California until 1972. They argued that it was probably there before that first detection date, so they pushed the date back to 1960. However, one could just as easily argue that pox went undetected for decades or that it appeared very suddenly around 1970. The only objec-

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tive way to group birds is to use the date when pox was first detected in coastal California.

The best evidence for a change in plumage redness over time that is presented by the authors was a weak but significant correlation between plumage hue of study skins and collection year. However, results of that analysis have to be viewed with caution. The authors examined skins in six museums. Anyone who has examined study skins in a collection is aware that the specimens are not collected uniformly over time and space. During any decade or set of decades, most specimens are likely to come from one active collector and from a single location. That can be a problem because, in coastal California, there can be large differences among local populations in mean male coloration (Hill 1993a). Zahn and Rothstein (1999) also documented substantial variation in mean male coloration among years and among local collecting sites in Santa Barbara, California. Thus, it is possible that birds collected early in the century happened to be collected mostly from local populations in which male coloration was bright on average, and that males were collected later in the century mainly from populations that averaged more drab in coloration. Such a collecting bias could have generated artificial time-related variation, regardless of any population-wide change in mean plumage redness over time. The possibility of sampling error could have been reduced by using only one specimen per collection site and collector per year, but then sample size would be greatly reduced. Furthermore, in that correlation analysis, year of collection was only weakly related to variation in plumage coloration ($r_s = 0.26$), so a small sampling bias could have accounted for the pattern.

So, we have weak evidence for a change in plumage color over time and only the most indirect link between a purported change in plumage coloration and exposure to pox. What about geographic variation in plumage coloration and pox? House Finches show substantial geographic variation in the mean plumage redness of males across North America, and the degree to which House Finches are exposed to pox also varies across their range. Zahn and Rothstein (1999) hypothesized that there is concordance between areas of high pox and areas where males average less red in plumage coloration. Unfortunately, poor methods were again employed. To quantify regional variation in plumage coloration, five different subjective descriptions of plumage coloration were used (the authors' own, two eastern banders', and two western banders'). No attempt was made to standardize among those independently derived systems and there was no way to know how various biases may have altered the data. That is equivalent to having five biologists describe the size of birds without any measuring device or without any standardization and then after the fact trying to decide how one observer's "pretty big" description compares to another's "above average" description.

The use of vague color descriptions for the analysis of geographic variation in coloration was unnecessary. In 1993, I published a detailed account of male plumage coloration based on hundreds of birds sampled in two populations in coastal California, at a high-elevation site on Hawaii Island, at a low-elevation site on Oahu Island, and in two eastern populations (Michigan and New York; Hill 1993a). That is the only study of geographic variation in plumage coloration of male House Finches that used a standardized color scoring method to compare males from different populations. Those would seem to be the ideal data to use in tests of hypotheses related to geographic variation in House Finch plumage coloration. However, the authors did not use those data (although they cite the paper elsewhere) and instead cite various obscure references and unpublished accounts that employ a hodge-podge of vague color descriptions. By ignoring my studies of geographic variation, the authors sidestep several key contradictory observations: a population at a high-elevation site in Hawaii (Pohakuloa, Hawaii Island) with no pox had mostly drab males; males at one feeding station in San Jose, California, where pox infection is common, were as bright as any eastern population; males at another feeding station 12 km away in San Jose, where pox was also common, were drab like males in Hawaii (Hill 1993a; Fig. 1). Even more so than the evidence for a link between pox and temporal change in plumage coloration, the evidence for a relationship between pox and geographic variation in mean male coloration is unconvincing.

One of the claims by Zahn and Rothstein (1999) that I found to be most unfounded was that "the high level of variation [in plumage coloration of male House Finches] is a new phenomenon . . . " First, it is not clear what the authors mean by "high level of variation." If the authors mean that before pox there were few or no yellow or orange males in populations, then all early descriptions of plumage coloration in House Finches contradict that statement. The best early descriptions of variation in the plumage coloration of male House Finches in the coastal California population are by Michener and Michener (1926, 1931), who described a full range of plumage variation, from pale yellow to bright red, among male House Finches banded during the 1910s and 1920s. In a series of House Finch specimens from California examined at the turn of century by Grinnell (1911), the full range of color variation from dull yellow to bright red was present. Moreover, Grinnell (1911) cites the collection of 18 male House Finches from the California–Arizona border, and again the full range of plumage variation from drab yellow to bright red was present. In 1939, Moore commented on the increased incidence of yellow and orange male House Finches on islands and stated that 73%

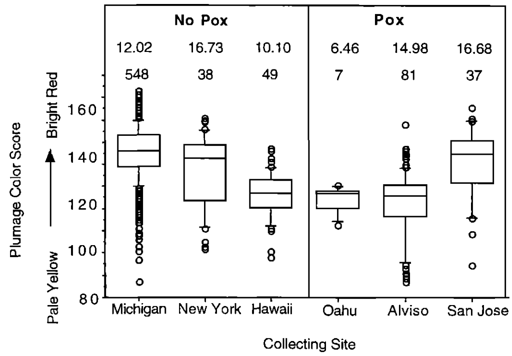

FIG. 1. Variation in the plumage coloration of male House Finches from single capture locations in Ann Abor, Michigan; Long Island, New York; Pohakuloa, Hawaii; Honolulu, Hawaii; Alviso, California; and San Jose, California. The three populations on the right were sampled in areas where avian pox infects House Finches. The three populations to the left were sampled in areas where House Finches are rarely exposed to pox. See Hill 1993 for details of samples locations, capture techniques, and methods for scoring plumage coloration. Plotted are the median, 25th and 75th percentiles, 90th and 10th percentiles, and outlying data points. Samples size and standard deviations for each population are given above the plots.

of males on San Clemente Island were orange or yellow. Moore (1939) also indicated that all populations have some yellow or orange males. All of those accounts came from years that predated the proposed occurrence of pox in House Finches in the western U.S. There is no doubt that male House Finches displayed a highly variable plumage before the date at which Zahn and Rothstein (1999) state that House Finches became exposed to pox.

Perhaps, though, the authors are not referring to the range of plumage variation (i.e. presence of some yellow and orange males) but rather specifically to the statistical parameter "variance." The authors, however, provide no test for difference in variance between pre- and postpox populations. The poor plumage scoring methods of Zahn and Rothstein (1999) in which all color variation is collapsed into three categories makes assessment of variance more difficult than it would be with a more detailed description of color. By comparing populations for which I recorded detailed plumage color data (Fig. 1), I was able to directly test the hypothesis that populations subjected to pox infection have higher variance than populations not subjected to pox infection. The hypothesis is rejected; among the populations that I sampled, males in Michigan, Hawaii, and Oahu had relatively low variance in plumage coloration whereas males in New York, and the two California populations had higher variance. The net result was that there was no consistent relationship between exposure to pox and variance in expression of plumage coloration (Fig. 1): the New York population (no pox) did not have significantly different variance than the two California populations (with pox) ($F = 0.0004$, df = 1 and 73, $P = 0.98$; $F = 0.63$, df = 1 and 117, $P = 0.43$; Bartlett's test) and the Michigan and Hawaiian populations (no pox) did not have significantly different variance than the Oahu population (pox) ($F = 3.01$, df = 1 and 553, $P = 0.08$; $F = 1.89$, df = 1 and 54, $P = 0.17$; Bartlett's test). I conclude that variance in plumage coloration among populations that are exposed to pox is not consistently greater than variance in plumage coloration among populations that are not exposed to pox.

The above criticisms concern problems with documenting temporal and spatial change in coloration. Perhaps the weakest part of the paper, however, is the discussion, where the authors argued that pox is the singular cause for variation in plumage coloration among male House Finches. The authors adopted what is, in my opinion, an unacceptable approach to hypothesis testing. Instead of subjecting the hypothesis that pox is the basis for plumage variation in male House Finches to rigorous attempts at falsification, the authors supported that favored hypothesis by dispensing with what they saw as the only alternatives. Basically, the authors set up a straw man (the idea that diet alone determines coloration), dispensed with it, and concluded that pox must be the explanation for drab House Finch plumage.

The authors dismissed the role of diet in expression of plumage coloration in male House Finches by citing poorly controlled aviary experiments conducted 40 years ago on other cardueline finch species (see Hill [1994] and Hudon [1994] for a previous discussion of this same issue). They never mentioned the extensive aviary feeding experiments with male House Finches that I have conducted and published (Hill 1992, 1993a, 1993b). The authors stated that carotenoids "may be abundant and varied in most habitats," but none of the studies that they cited present any data on that point. To the contrary, the only published study that directly measured abundance of carotenoids in natural environments found that carotenoids were limiting (Slagsvold and Lifjeld 1985), which was not mentioned by the authors. The authors stated that "there is no evidence that some males have access to certain dietary resources from which others are excluded." Again, that is contrary to published evidence. Hill and Montgomerie (1994) provided evidence that there are differences among males in access to nutritional resources during molt. The authors then stated "Nor does the diet hypothesis account for the sudden shift in the proportion of red south-coastal California males in the mid-1900's, which would require evidence of a major perturbation of plant species." I think that any botanist who has lived in southern California over the last several decades would attest to rather massive changes in the biota of the region starting around the turn of the century.

Throughout their discussion, the authors give simple answers based on little or no data to very complex questions. That overly simplistic approach is most obviously absurd when the authors begrudgingly admit that perhaps factors other than pox can also affect plumage coloration: "Non-red variants existed historically and continue to do so today in populations where male plumage is predominantly red, which may indicate that color change can also result from other sources of weakened body condition in addition to pox." However, in the next sentence, they retreat to the idea that pox is the final explanation: "It could also be that the disease, which has been present in other species for a longer time than in House Finches, may have been present in House Finches but was not detected because of low virulence and an absence of tumors."

Why does it really matter if the poor methods and faulty logic of Zahn and Rothstein (1999) lead to erroneous conclusions regarding plumage coloration in the House Finch? Over the last decade, behavioral and evolutionary biologists have become increasingly interested in carotenoid pigmentation as an honest signal of male quality (Andersson 1994, Olson and Owens 1998). Central to that issue is the proximate basis for variation in expression of carotenoid-based integumentary coloration. On the basis of the growing number of experimental studies in that field (summarized in Hill [1999] and Olson and Owens [1998]), evidence strongly suggests that a variety of factors combine to determine expression of carotenoid-based plumage coloration. For male House Finches, those factors include dietary access to carotenoids (Hill 1992, 1993a, b), access to nutrition during molt (Hill and Montgomerie 1994, Hill 2000), and degree of parasitism (Brawner 2000, Hill and Brawner 1998, Thompson et al. 1997). Coccidians, protozoan parasites of the gut, have a direct negative effect on carotenoid absorption across the gut lining (Allen 1986, 1987, 1992; Ruff et al. 1974) and hence carotenoid pigmentation in the House Finch (Brawner 2000). Other diseases such as mycoplasmosis (a bacterial infection) also have a negative effect on expression of plumage coloration in this species (Brawner 2000). And yes, evidence also suggests that avian pox has a significant negative effect on House Finch plumage coloration (Thompson et al. 1997). But, the assertions made by Zahn and Rothstein (1999) that temporal or geographic variation in incidence of avian pox among House Finches is the primary or sole source of temporal or geographic variation in male plumage coloration, and that variation in male plumage coloration is a recent phenomenon in male House Finches, are not only unjustified, they contradict the careful research in this field showing the true complexity of control of ornamental plumage coloration.

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House Finches Are Not Just What They Eat: A Reply To Hill

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The coevolutionary interactions of pathogens and their hosts are likely to be a widespread mechanism that results in the maintenance of genetic variation. Alternatively, highly variable species may be in a transient state, with their variation reflecting directional selection and new selection pressures. With those insights in mind, we set about to study the House Finch (*Carpodacus mexicanus*), some of whose populations are arguably the most variable among North American birds with regard to plumage coloration in males of the same age. In addition, we were also attracted to House Finches by our observations and those of others (McClure 1989, Power and Human 1976) that this species is highly unusual not only for its color variation, but for its remarkably high incidence of disease, particularly avian pox, which of course raised the question of whether pathogens and plumage color might be related. Lastly, the possibility of recent changes in disease incidence was raised by the first published report (Power and Human 1976) of pox disease in mainland populations of this common species, which reported a severe outbreak in 1972. Accordingly we set out to determine whether there is any evidence of a link between plumage color variation and pox and whether extreme variation in color and high pox-incidence might be new conditions.

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